# A Review of the Biology of *Acacia suaveolens* (Smith) Willd. (Mimosaceae)

DAVID A. MORRISON

(Communicated by P. J. MYERSCOUGH)

Published and original data on a number of aspects of the biology of *Acacia suaveolens* are presented, including: taxonomy, geographical distribution, climatic, topographic, and altitudinal limitations, substratum, communities, gregariousness; response to biotic factors; performance in various habitats, effect of frost, drought, and waterlogging, morphology, chromosomes, physiology, biochemistry, perennation and reproduction, phenology, flowering and pollination, seed production and dispersal, viability of seeds and germination, seedling morphology, mycorrhiza, animal feeders and parasites, plant diseases and parasites, and history and conservation status.

D. A. Morrison, Department of Applied Biology, New South Wales Institute of Technology, P.O. Box 123, Broadway, Australia 2007; manuscript received 9 December 1986, accepted for publication 22 April 1987.

## INTRODUCTION

In 1941 the British Ecological Society began publishing a series of papers on the 'Biological Flora of the British Isles' (Anon., 1941), a series that is still being actively published. This series was intended to be an introductory reference source of published and unpublished data on various aspects of the biology of the plant species occurring in Great Britain.

No similar series has been undertaken for Australian plants, partly, at least, because very few data exist for most of the species. However, extensive data do exist for a number of the more common species, particularly of the genera *Eucalyptus* and *Acacia*. This paper is an attempt to summarize the published data on one particular species, *Acacia suaveolens* (Smith) Willd., that is common in south-eastern Australia and for which considerable data do exist. The data are arranged in the format used by the British Ecological Society in publishing their Biological Flora, and I have attempted to collate whatever data exist concerning *A. suaveolens* for each of the aspects covered in that series (see Anon., 1941), and to contribute original data for aspects for which published data are not available. The references cited are mainly a subset of the bibliography of 186 sources of data on *A. suaveolens* listed in Morrison (1986).

## DESCRIPTION AND TAXONOMY

*Acacia suaveolens* (Smith) Willd., *Sp. Pl.* 4:1050 (1806)
[*Mimosa suaveolens* Smith, *Trans. Linn. Soc. Lond.* 1:253 (1791) non Salisb. (1796); *Mimosa obliqua* Lam., *J. Hist. Nat. Paris* 1:89 (1792) non H. H. Wendl. (1798); *Mimosa ambigua* Salisb., *Prodr. Stirp.* 325 (1796); *Mimosa angustifolia* Jacq., *Pl. Hort. Schoenbr.* 3:74 (1798); *Acacia angustifolia* (Jacq.) H. H. Wendl., *Comm. Acac.* 34 (1820); *Acacia suaveolens* var. *platycarpa* DC, *Prodr.* 2:453 (1825); *Phyllodoce suaveolens* (Smith) Link, *Handbuch* 2:133 (1831); *Phyllodoce angustifolia* (Jacq.) Link, *Handbuch* 2:133 (1831); *Hecatandra suaveolens* (Smith) Raf., *Sylva Tellur.* 120 (1838) ]

Subgenus *Phyllodineae* (DC) Ser.; Section *Phyllodineae* DC; Subsection *Racemosae* (Benth.) Maiden

Usually erect, slender, glabrous, little-branched, open shrub to 2(-3)m high; bark smooth, (bluish-)green. *Branchlets* terete below but acutely triquetrous above due to decurrencies, sometimes almost flattened, glabrous, brownish-green or sometimes glaucous, new growth often pinkish. *Phyllodes* alternate, erect, glaucous, coriaceous, glabrous, flat, straight or rarely slightly falcate, narrow-oblong to linear-lanceolate, acute or obtuse, acuminate or mucronate, narrowed towards the base, (5-)7-12(-20)cm long, (2-)3-7(-10)mm wide, (9-)13-27(-35) times as long as broad, one-nerved more or less central, margins thickened, yellowish-brown; pulvinus 1-2mm long; small, flat, elongated, non-porate gland (1-)2-3(-4)mm from base of phyllode, sometimes another gland at tip. *Inflorescence* of globular heads 5-8mm in diameter, each of (3-)4-7(-12) flowers, in glabrous, axillary, often crowded, (5-)6-8(-12)-branched racemes; rhachis 1-2(-3)cm long, slender; peduncles 2-5mm long, slender; flower heads andromonoecious, usually twice as many male as hermaphrodite flowers; before development, racemes enclosed by imbricate, scarious, fimbriate, ovate, obtuse, pale yellow-brown, pink-tipped bracts to 2.5mm long, crowded at base of axis, with larger ones subtending individual peduncles, all deciduous before anthesis. *Flowers* actinomorphic, (4-)5(-6)-merous, creamy to pale lemon-yellow, protogynous, sweetly-scented. *Sepals* free, thin, linear-spathulate, acuminate, glabrous with a few hairs at the tip, 1.2-1.3mm long. *Petals* thin, free, ovate-oblong, glabrous, 1.7-3mm long, 0.7-1mm wide, less than twice as long as the calyx. *Stamens* (35-)40-55(-80), 3-5mm long; anthers small, almost round, bilobed with 4 loculi per lobe. *Ovary* unilocular, central, superior, yellow-brown, oblong, laterally compressed, acuminate, glabrous, with (4-)5-7(-8) anatropous basally-attached ovules. *Style* yellow-brown, filiform, bent, up to twice as long as the stamens; stigma simple, terminal, acute. *Pollen* grains yellow, non-reticulate, 4-porate, pores placed towards the angles of the grains, 4-furrowed; grains aggregated into polyads of 16, long equatorial diameter of the polyad 52-64μm, 1 polyad per locule. *Legume* stalked, glaucous, purplish-red at fertilization, turning bluish-green, often reddish-brown over the seeds, brown when open at maturity, glabrous, coriaceous, pruinose, (elliptic-)oblong, obtuse, apiculate, laterally compressed but slightly raised over the seeds, 2-4(-5)cm long, (10-)12-20mm wide, twice as long as wide, margins thickened. *Seeds* smooth, shiny, dark brown to brownish-black (rarely maroon), transverse, (elliptic-)oblong, 5-8mm long, 2.5-4.5mm wide, 2-3 times as long as wide; areole closed, 3-4.5mm long, 0.6 times the length of the seeds; funicle 1.5-2mm long, filiform till nearly mature then thickened into a slightly oblique, fleshy, 1-3(-4)-folded aril covering the hilar end, same colour as the seeds; no albumen present.

Variable in erectness, height, phyllode axillary angle, phyllode shape and size, and number of flowers per inflorescence, but most of this has no apparent genetic basis. In the Myall Lakes area, populations of plants with very narrow phyllodes (< 2mm wide; Armitage, 1977) are common in the sclerophyllous forest community on the Holocene sand, and this may have a strong genetic component. In the Grampians, populations with phyllodes held conspicuously close to the stem and a small rootstock can be found in the deeper sands on the west-facing slopes. Along the New South Wales coast north of Sydney, plants with a prostrate, spreading habit and much broader phyllodes are often found on thin soils on exposed headlands. Elliot and Jones (1982) also report that a form with a cream band on each side of the phyllode midvein and flowers with a deeper yellow is often cultivated, but that it 'must be propagated from cuttings to retain the variegation'.

## GEOGRAPHICAL DISTRIBUTION

*A. suaveolens* is endemic to the southeastern coast of the Australian mainland, around the coast of Tasmania, and on the larger off-shore islands (Fig. 1). It is generally restricted to the coast, although it does occur inland, notably in the Sydney Basin, in the Grampians, and at the South Australia-Victoria border.
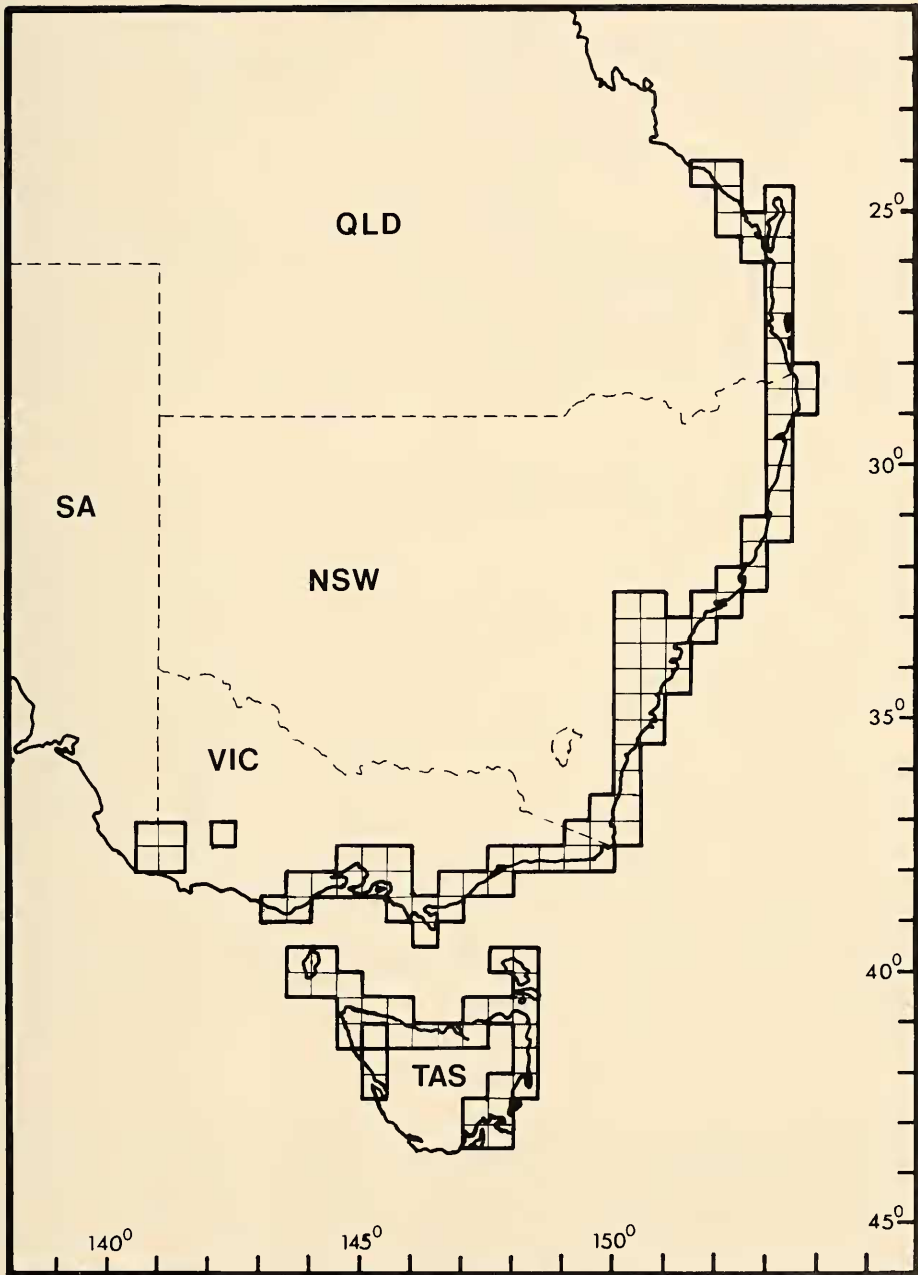
Fig. 1. Known distribution of *Acacia suaveolens*. Each outline represents at least one record on the national 0.5° × 0.5° grid. Data from dried specimens held at AD, BRI, CANB, CBG, HO, MEL, NSW, PERTH, and SYD (codes after Holmgren *et al.*, 1981).

In the literature, populations have also been recorded on the Victorian coast east of the South Australian border (Churchill and de Corona, 1972; Costermans, 1981), east of the Grampians (Churchill and de Corona, 1972; Beauglehole, 1980b; Maslin and Pedley, 1982), in the Albury district (Jacobs and Pickard, 1981; Maslin and Pedley, 1982), and in the northern tablelands of New South Wales (Simmons, 1981; Maslin and Pedley, 1982), but these records have not been confirmed and are not supported by herbarium voucher specimens (Beauglehole, 1980a; Morrison *et al.*, 1983).

## CLIMATIC, TOPOGRAPICAL AND ALTITUDINAL LIMITATIONS

As a result of its large latitudinal (24°26′S to 43°15′S) and altitudinal (0-950m) range, *A. suaveolens* experiences a wide range of climatic extremes (Table 1), and does not appear to show any particular climatic preferences. It also does not exhibit any climatically-determined slope preferences. Burrough *et al.* (1977) have found plants growing at both extremes of a strong gradient of sites varying from a strongly positive to a balanced precipitation/evaporation budget over a short distance on the New South Wales central coast.

TABLE 1

*Long-term temperature and precipitation extremes within the geographical distribution of* Acacia suaveolens
*Data from Australian Bureau of Meteorology (1975a-e) for a total of 163 meteorological stations*

| Climatic parameter | | Value | Meteorological station |
|---|---|---|---|
| Mean annual maximum temp.: — max. | | 28.5°C | Tabbimoble S.F., N.S.W. |
| | min. | 13.4°C | Tasman Is. Lighthouse, Tas. |
| Highest mean monthly maximum temp.: — max. | | 31.6°C | Tabbimoble S.F., N.S.W. |
| | min. | 10.2°C | Tasman Is. Lighthouse, Tas. |
| Mean annual minimum temp.: — max. | | 17.3°C | Tabbimoble S.F., N.S.W. |
| | min. | 5.5°C | Geeveston (Forestry), Tas. |
| Lowest mean monthly minimum temp.: — max. | | 22.8°C | Tabbimoble S.F., N.S.W. |
| | min. | 0.0°C | Geeveston (Forestry), Tas. |
| Mean annual rainfall: — max. | | 1814 mm | Alstonville Res. Stn., N.S.W. |
| | min. | 538 mm | Geelong (S.E.C.), Vic. |
| Mean annual no. raindays: — max. | | 235 | Strahan (Vivian St), Tas. |
| | min. | 57 | Waterloo, Qld. |

Populations are most commonly found within a few kilometres of the coast, and below an altitude of 300m. The only places where this species is recorded above 500m (to 600m in the McPherson Range, to 950m in the Blue Mountains, to 650m in the Budawang Range) are where the upland sandstone soils of the Great Dividing Range are contiguous with the sandy coastal plain.

## SUBSTRATUM

On the mainland, *A. suaveolens* is most commonly found on the coastal Quaternary sands. The northern boundary of the distributional range is near the northern boundary of the lime-free sandy and sandy-loam soils that form the dominant soil type along the eastern Australian coast. However, coastal populations are occasionally reported from the perimeter of clay soils over sandstone (e.g. Webb, 1981); and on Wilsons Promontory the species is also found as a rare occurrence on the perimeter of sandy soils over Devonian granite (Gillham, 1960; Ashton and Webb, 1977).

Inland along the eastern coast, the species occurs on sandy soils over Jurassic sandstone in the McPherson Range, over Triassic sandstone in the Sydney Basin, over Devonian sandstone in the Budawang Range, and over Ordovician sandstone near Orbost. It is not found on the inland sandstone areas which are isolated from the coastal sandy soils.

It has also been recorded from acid Tertiary rhyolite on the Lamington Plateau (McDonald and Elsol, 1984) and on Mt Coolum (Sharpe and Batianoff, 1985).

Between Lorne and Warrnambool, populations are found on inland sandy soils over Tertiary sandstone, rather than on the uplifted Cretaceous shale of the Otway Range adjacent to the coast. The species does not occur on the coastal soils derived from the Tertiary limestone and Quaternary volcanics west of Warrnambool; and the isolated populations in the Grampians occur on Quaternary sand and on sandy soils over Devonian sandstone. Near the Victoria-South Australia border, populations are found on the inland siliceous Quaternary sands and sandy soils over Tertiary sandstone, but do not occur on the calcareous Quaternary sands nearer to the coastline.

In Tasmania, this species is common on sandy soils over the many sandstones (e.g. Silurian, Permian, Triassic, Tertiary) which form most of the northern and eastern coastline, but it only occurs sporadically on the Tertiary and Middle Proterozoic sandstones along the northwestern coastline. On the Tasman Peninsula, it is also found on thin sandy soils over Jurassic dolerite (Kirkpatrick, 1977b). In the Furneaux Group, plants occur on sandy soils over both Silurian sandstone and Devonian granite, as well as on granitic colluvium (Kirkpatrick, 1977b); and on King Island, plants are found on Middle Proterozoic sandstone soils.

*A. suaveolens* has been recorded from the following soil groups: — lithosols (Ashton and Webb, 1977), siliceous sands (Parsons, 1966; Firth, 1969; Durrington, 1977; Kirkpatrick, 1977a, 1977b; Benson and Fallding, 1981; Forbes *et al.*, 1982; Opie *et al.*, 1984), earthy sand (Buchanan and Humphreys, 1980), yellow earths (Benson and Fallding, 1981), humus podzols (Myerscough and Carolin, 1986), and peaty podzols (Parsons, 1966). However, it is most commonly found on siliceous sand podzols, of various colours and stages of differentiation: e.g. poorly-developed (Kirkpatrick, 1973; Myerscough and Carolin, 1986), moderately-developed (Clark, 1975; Thatcher and Westman, 1975), well-developed (Groves and Specht, 1965; Kirkpatrick, 1975; Ingwersen, 1976; Ashton and Webb, 1977; Burrough *et al.*, 1977; Clifford and Specht, 1979; Buchanan and Humphreys, 1980).

These soils may be very shallow (e.g. Cambage, 1923; Petrie, 1925; Hannon and Evans, 1963; Kirkpatrick, 1977b; Auld and Myerscough, 1986) but are usually quite deep (e.g. Groves and Specht, 1965; Ingwersen, 1976; Durrington, 1977; Kirkpatrick, 1977b; Clifford and Specht, 1979; Opie *et al.*, 1984; Myerscough and Carolin, 1986). The soils are predominantly freely-draining, but are occasionally seasonally waterlogged or permanently moist (see below). The surface pH has been recorded from 4.3-6.9 (Davis, 1941a; 1941b; Gillham, 1960; Parsons, 1966; Siddiqi *et al.*, 1972; Burrough *et al.*, 1977; Kirkpatrick, 1977b; Buchanan and Humphreys, 1980). The soils are extremely infertile, being relatively more fertile in the wetter habitats. The surface loss-on-ignition varies from 0.9-30.0% (Pidgeon, 1938; Davis, 1941a; 1941b; Ingwersen, 1976; Burrough *et al.*, 1977; Myerscough and Carolin, 1986); and total nitrogen ranges from 0.02-0.18% (Hannon, 1956; Siddiqi *et al.*, 1972; 1976; Myerscough and Carolin, 1986). Total phosphorus varies from 0.001-0.01% (Beadle, 1962; Parsons, 1966; Myerscough and Carolin, 1986), with 'available' water-soluble phosphorus ranging from 0.0002-0.0013% (Siddiqi *et al.*, 1972; 1976; Ingwersen, 1976). The exchangeable calcium is reported to be in the range 0.52-4.0 meq.%, the exchangeable potassium from 0.06-0.95 meq.%, the exchangeable magnesium from 0.2-1.77 meq.%, and the exchangeable sodium from 0.05-0.95 meq.% (Siddiqi *et al.*, 1972; 1976; Ingwersen, 1976; Burrough *et al.*, 1977; Myerscough and Carolin, 1986).

*A. suaveolens* grows well in the laboratory in a range of soil types with higher fertility levels than those on which it is normally found in the wild (Beadle, 1962); and the absence of plants from higher fertility soils has been ascribed to an inability to compete with faster-growing species under these conditions (Beadle, 1962).

## COMMUNITIES

    *A. suaveolens* can be regarded as a short-lived pioneer species (Clemens and Franklin, 1980), and it often occurs in early successional communities (but not in the early exposed stages) (Pidgeon, 1938; 1940) or in early phases of regeneration cycles. As a result, the presence of the species in a community is very dependent on the past history of disturbance, especially in relation to fire. The species has been recorded from a wide variety of communities, including forests, woodlands, shrublands, heaths, and sedgelands (Table 2).

### TABLE 2

*Plant communities in which* Acacia suaveolens *has been recorded*

| Alliance* | Suballiance* | Structural form [+] | Area | Reference[†] |
|---|---|---|---|---|
| *Eucalyptus pilularis* | a) *Eucalyptus pilularis* | woodland | Bulli, N.S.W. | (9) |
| | b) *Eucalyptus pilularis-* | open-forest | Nth Stradbroke Is., Qld. | (31) |
| | *Eucalyptus intermedia-* | open-forest | Moreton Is., Qld. | (10) |
| | *Eucalyptus siderophylla* | | | |
| | c) *Eucalyptus pilularis-* | open-forest | Myall Lakes, N.S.W. | (2), (21) |
| | *Angophora costata* | open-forest | Sydney, N.S.W. | (15) |
| *Eucalyptus botryoides* | | low open-forest | Sydney, N.S.W. | (5), (15) |
| | | woodland | Sydney, N.S.W. | (26) |
| | | low woodland | Sydney, N.S.W. | (4) |
| *Eucalyptus gummifera-* | a) *Eucalyptus gummifera-* | open-forest | Sydney, N.S.W. | (23) |
| *Eucalyptus racemosa-* | *Eucalyptus racemosa-* | low open-forest | Sydney, N.S.W. | (5), (23) |
| *Eucalyptus sieberi* | *Angophora costata* | low open-forest | Barren Grounds, N.S.W. | (6) |
| | | woodland | Sydney, N.S.W. | (2), (5) (15) (23), (26) |
| | | woodland | Barren Grounds, N.S.W. | (6) |
| | | woodland | Jervis Bay, N.S.W. | (17) |
| | b) *Eucalyptus sieberi-* | open-forest | Sydney, N.S.W. | (3), (15) |
| | *Eucalyptus piperita-* | open-forest | Fitzroy Falls, N.S.W. | (6) |
| | *Eucalyptus racemosa* | low open-forest | Bulli, N.S.W. | (8) |
| | | low open-forest | Macquarie Pass, N.S.W. | (11) |
| | c) *Eucalyptus eximia-* | woodland | Sydney, N.S.W. | (3) |
| | *Eucalyptus punctata* | woodland | Bulli, N.S.W. | (9) |
| *Eucalyptus globoidea* | | open-forest | East Gippsland, Vic. | (13) |
| | | woodland | East Gippsland, Vic. | (13) |
| *Eucalyptus baxteri* | | open-forest | South Australia | (29) |
| | | low open-forest | South Australia | (32) |
| | | woodland | Wilsons Promontory, Vic. | (1) |
| | | low woodland | Wilsons Promontory, Vic. | (24) |
| *Eucalyptus amygdalina* | | open-forest | Schouten Is., Tas. | (16) |
| | | woodland | Tasman Peninsula, Tas. | (18) |
| *Banksia aemula* | | low open-forest | Nth Stradbroke Is., Qld. | (31) |
| | | woodland | Sydney, N.S.W. | (26) |
| | | open-woodland | Nth Stradbroke Is., Qld. | (30) |
| | | tall shrubland | Moreton Is., Qld. | (10) |
| | | tall open-shrubland | Nth Stradbroke Is., Qld. | (7) |
| | | tall open-shrubland | Moreton Is., Qld. | (10) |
| | | closed-heath | Moreton Is., Qld. | (10) |
| | | closed-heath | Myall Lakes, N.S.W. | (21) |
| | | closed-heath | Sydney, N.S.W. | (27), (28) |
| *Banksia ericifolia* | | open-scrub | Sydney, N.S.W. | (5) |
| | | closed-heath | Sydney, N.S.W. | (28) |
| | | open-heath | Macquarie Pass, N.S.W. | (11) |
| *Banksia oblongifolia* | | closed-heath | Sydney, N.S.W. | (23) |
| | | open-heath | Myall Lakes, N.S.W. | (21) |
| | | open-heath | Sydney, N.S.W. | (27) |
| *Banksia robur* | | sedgeland | Sydney, N.S.W. | (5), (15) |
| *Banksia marginata* | | closed-heath | Wilsons Promontory, Vic. | (14) |
| | | closed-heath | Rocky Cape, Tas. | (12) |
| | | closed-heath | Ocean Beach, Tas. | (19) |
| | | open-heath | Schouten Is., Tas. | (16) |
| *Leptospermum myrsinoides* | | closed-heath | Wilsons Promontory, Vic. | (1) |

TABLE 2 (Cont'd.)

| Alliance* | Suballiance* | Structural form [+] | Area | Reference† |
|---|---|---|---|---|
| *Leptospermum scoparium* | | low open-shrubland | Western Port, Vic. | (22) |
| | | closed-heath | Flinders Is., Tas. | (20) |
| *Casuarina littoralis-* *Banksia oblongifolia* | | closed-heath | Northern coastal N.S.W. | (2) |
| *Casuarina distyla* | | closed-heath | Sydney, N.S.W. | (2) |
| | | closed-heath | Mt. Wilson, N.S.W. | (25) |
| | | closed-heath | Bowen Is., N.S.W. | (17) |
| | | open-heath | Sydney, N.S.W. | (23) |
| *Melaleuca squarrosa* | | open-scrub | Wilsons Promontory, Vic. | (24) |
| | | open-heath | Wilsons Promontory, Vic. | (24) |

*   after Beadle (1981)
+   after Specht (1970)
†   Sources of data: — (1) Ashton and Webb (1977); (2) Beadle (1981); (3) Benson (1981a); (4) Benson (1981b); (5) Benson and Fallding (1981); (6) Burrough *et al.* (1977); (7) Clifford and Specht (1979); (8) Davis (1941a); (9) Davis (1941b); (10) Durrington (1977); (11) Fallding and Benson (1985); (12) Firth (1969); (13) Forbes *et al.* (1982); (14) Gillham (1960); (15) Hannon (1956); (16) Harris and Kirkpatrick (1982); (17) Ingwersen (1976); (18) Kirkpatrick (1973); (19) Kirkpatrick (1977a); (20) Kirkpatrick (1977b); (21) Myerscough and Carolin (1986); (22) Opie *et al.* (1984); (23) Outhred *et al.* (1985); (24) Parsons (1966); (25) Petrie (1925); (26) Pidgeon (1940); (27) Siddiqi *et al.* (1972); (28) Siddiqi *et al.* (1976); (29) Specht (1972); (30) Specht *et al.* (1977); (31) Thatcher and Westman (1975); (32) Whibley (1980)

The forest communities are usually found only on deep coastal sand masses, and have an open, heathy understorey. The woodlands also have a heath rather than a scrub understorey, and usually occur on the shallower soils. The heath communities vary from open to closed, and include both dry and wet heaths. Plants also occur occasionally in ground-water heaths, and sporadically around the edges of swamps in the northern areas (e.g. White, 1945; Hannon, 1956). The species is not found in closed coastal communities such as the exposed *Leptospermum laevigatum* and *Acacia sophorae* closed-scrubs which front many of the beaches, occurring instead in the more open woodlands or heaths slightly further inland (e.g. Giliham, 1960). Plants do, however, occasionally occur in exposed headland heaths on thin sandy soils over sandstone along the New South Wales coast (Beadle, 1981) and over dolerite on the Tasman Peninsula (Kirkpatrick, 1977b), and also on leached sands in exposed situations within the salt spray zone along the northern and eastern coasts of Tasmania (Kirkpatrick, 1977b). The species also does not appear in the coastal closed-grasslands, but plants are occasionally found in understoreys with clumped grasses.

The community dominants vary with the geographical area (Table 2) and substratum. In Queensland and northern New South Wales on low fertility soils, *A. suaveolens* is found in *Eucalyptus intermedia* open-forests, and also in the *Banksia aemula* low open-forests and tall open-shrublands on the deep sand coastal islands. On more fertile soils, but not usually in valleys, it occurs in *Eucalyptus pilularis* open-forests.

On the New South Wales central coast, it is found in *Eucalyptus botryoides* low open-forests or woodlands in the higher fertility areas on the hind-dunes, and in *E. pilularis* open-forests and low open-forests on the deep coastal sand masses and higher-fertility inland soils. More commonly, it occurs on less fertile soils in low open-forests or woodlands dominated by *Eucalyptus gummifera* (in wetter areas), *Eucalyptus sieberi* (further south), *Eucalyptus racemosa* (at higher altitudes), *Eucalyptus piperita* (in more fertile spots), and *Angophora costata* (ubiquitous). It is also common in *B. aemula* low open-forests, heaths, and shrublands on sand throughout the New South Wales coast. It is also common on sand and sandstone in dry heaths of *Banksia ericifolia* and *Casuarina distyla*, and with *Casuarina littoralis* on exposed sandy headlands. In wetter heaths, it occurs with *Banksia oblongifolia*, and occasionally with *Banksia robur*.

In Victoria, the open-forests and woodlands are dominated in the east by *Eucalyptus globoidea* (on more fertile soils) and *E. sieberi* (on less fertile soils), and in the west (and also in South Australia) by *Eucalyptus baxteri* (on the less fertile soils) and *Eucalyptus obliqua* (on the more fertile soils). In eastern Victoria, the species also occurs in *Leptospermum myrsinoides* heaths, and, in wetter more saline areas, in heaths and thickets dominated by *Melaleuca squarrosa*. On soils derived from granite, plants are occasionally found around the edges of *Banksia marginata* heaths.

In Tasmania, the species is very common in *B. marginata* heaths, especially on sand. It is also found in woodlands and open-forests of *Eucalyptus amygdalina*, often with *Eucalyptus viminalis* and *Eucalyptus tenuiramis* in more fertile areas. On the west coast, it is also a rare occurrence in open-scrub formations of *Eucalyptus nitida* and *Eucalyptus ovata* in low-fertility sand deposits, often in isolated patches among low heaths on exposed headlands.

Within the communities, *A. suaveolens* may be associated with a wide range of species. For example, in eucalypt forests along the southern coast of New South Wales and east coast of Victoria its occurrence has been found to correlate positively with 27 angiosperm species, notably *Eucalyptus gummifera*, *Leptospermum attenuatum*, *Caustis flexuosa*, and *Ricinocarpos pinifolius* (Table 3).

## TABLE 3

*Percentage frequency of occurrence with ( + ) and without (–)* Acacia suaveolens *of some angiosperm plants associated with A. suaveolens at three sites covering two eucalypt alliances in which* A. suaveolens *is commonly found. Data from Miller (1972), Ingwersen (1976), and Forbes* et al. *(1982) respectively*

| Species | E. gummifera — E. racemosa — E. sieberi Alliance Royal National Park (+) | (−) | $x^2$ | | Jervis Bay Territory (+) | (-) | $x^2$ | | E. globoidea Alliance East Gippsland (+) | (-) | $x^2$ | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| [No. quadrats] | [ 9] | [80] | | + | [23] | [52] | | | [34] | [71] | | |
| *Acacia oxycedrus* | — | — | | + | — | — | | | 29 | 7 | 9.40 | ** |
| *Actinotus minor* | 0 | 1 | | | 35 | 12 | 5.67 | * | — | — | | |
| *Banksia ericifolia* | 22 | 10 | | | 39 | 15 | 5.13 | * | — | — | | |
| *Banksia serrata* | 56 | 84 | | | 65 | 42 | 4.96 | * | 79 | 69 | | |
| *Bossiaea ensata* | — | — | | | 48 | 12 | 11.98 | *** | — | — | | |
| *Cassytha glabella* | 33 | 16 | | | 26 | 21 | | | 74 | 49 | 5.51 | * |
| *Caustis flexuosa* | 78 | 31 | 7.61 | ** | 35 | 13 | 4.53 | * | 24 | 28 | | |
| *Correa reflexa* | — | — | | | 26 | 8 | | | 65 | 38 | 6.57 | * |
| *Dampiera stricta* | — | — | | | 61 | 8 | 24.72 | *** | 88 | 83 | | |
| *Darwinia taxifolia* | — | — | | | 30 | 10 | 5.06 | * | — | — | | |
| *Empodisma minus* | — | — | | | — | — | | | 29 | 8 | 7.82 | ** |
| *Epacris microphylla* | 22 | 1 | | | 39 | 6 | 13.21 | *** | — | — | | |
| *Eucalyptus gummifera* | 78 | 34 | 5.90 | * | 74 | 38 | 8.02 | ** | 21 | 14 | | |
| *Eucalyptus racemosa* | — | — | | | 43 | 21 | 4.16 | * | — | — | | |
| *Gompholobium huegelii* | — | — | | | — | — | | | 32 | 10 | 8.19 | ** |
| *Hardenbergia violacea* | 44 | 13 | 6.23 | * | 17 | 25 | | | — | — | | |
| *Hibbertia fasciculata* | — | — | | | — | — | | | 29 | 8 | 7.82 | ** |
| *Hypolaena fastigata* | — | — | | | 4 | 6 | | | 32 | 3 | 18.49 | *** |
| *Isopogon anemonifolius* | 11 | 10 | | | 35 | 8 | 8.71 | ** | — | — | | |
| *Leptospermum attenuatum* | 67 | 25 | 6.79 | ** | 52 | 10 | 16.48 | *** | 47 | 23 | 6.53 | * |
| *Leucopogon collinus* | — | — | | | — | — | | | 62 | 18 | 19.83 | *** |
| *Lycopodium fastigatum* | — | — | | | 30 | 12 | 3.97 | * | — | — | | |
| *Monotoca scoparia* | — | — | | | 13 | 6 | | | 53 | 21 | 10.80 | ** |
| *Persoonia caleyi* | — | — | | | 43 | 8 | 13.45 | *** | — | — | | |
| *Platysace linearifolia* | 89 | 68 | | | 39 | 10 | 9.15 | ** | — | — | | |
| *Ricinocarpos pinifolius* | 22 | 40 | | | 35 | 12 | 5.67 | * | 59 | 24 | 12.26 | *** |
| *Themeda australis* | — | — | | | 13 | 44 | | | 26 | 11 | 3.92 | * |

+  Values indicate statistical association between the species and *A. suaveolens* at that site. Lack of any details indicates that the association was NS at $P<0.05$, or that it was not tested because one of the four values in the $2\times2$ contingency table was $<1$ or more than one was $<5$. * $0.01<P<0.05$, ** $0.001<P<0.01$, *** $P<0.001$.

‡  Missing data indicate that the species was not recorded at that site.

## Gregariousness

Population size and density vary markedly with the past history of disturbance by fire. Monospecific stands of up to 250 plants/m$^2$ have been recorded in mature recently-burnt populations, although population density is usually in the range 0.8-6 plants/m$^2$ (Auld, 1984). In older less-disturbed habitats, plants are usually widespread but not abundant. As the plants are relatively short-lived and do not normally regenerate without fire (Auld and Myerscough, 1986; Auld, 1987), density decreases with age of the population.

## Response to Biotic Factors

Plants without rootstocks are destroyed by even the mildest fires. However, these fires render the seed coat permeable to water, and the seeds in the soil then imbibe and germinate if suitable rains fall (Bradstock, 1981; Auld, 1986c). Thus, if plants are old enough to have produced seed, the species will readily regenerate strongly immediately following a fire (e.g. Specht, 1975; Siddiqi *et al.*, 1976; Harrold, 1979); and *A. suaveolens* is often the major understorey species (commonly with *Pteridium esculentum* and *Imperata cylindrica*) in communities which have been frequently burnt.

This species does not respond well to disturbances other than fire. It does not regenerate following disturbance by sand mining without being treated with fertilizer (Clark, 1975; Thatcher and Westman, 1975), but it does compete well with exotic grass cover after this disturbance (Thatcher and Westman, 1975). Gillham (1960) has noted that this species is characteristic of the unaffected areas of sea-bird rookeries but does not occur in areas which have been dug or trampled by the birds. Similarly, Yates (1976) found that it does not regenerate well in easements under electrical transmission lines, attributing this to continued disturbance from maintenance, a higher water table, and the use of herbicides.

## Performance in Various Habitats

The size which plants attain varies greatly between habitats, as does the size at which they begin to flower and the number of inflorescences and fruits produced per year. Death rates vary between sites, apparently depending on the rate at which the soil dries out during summer (Auld, 1987), being greater in thin sandy soils compared with deep sands. Auld (1984) has also reported between-site variability in seed weight and seed viability.

Seed production is reduced through predation by the weevil *Melanterius corosus*, and the extent of this predation varies markedly between sites. Auld (1983) and Auld and Myerscough (1986) found losses to vary from 10-61%, with a mean of 47%, at six sites during several fruiting seasons. Populations which suffer from this weevil predation have only been found north of Jervis Bay in New South Wales; and the predation is usually more prevalent in larger populations, with scattered populations of only a few individuals commonly being free from predation.

Leaf area does not vary (range 8.0-8.3 cm$^2$) when grown in the laboratory in a range of soil types (Beadle, 1962), but total dry weight of the plants (as well as root nodulation) is reduced when plants are grown in swamp soils as opposed to the lower-nutrient eucalypt forest soils (Hannon, 1956).

In cultivation, plants will grow in light from filtered sun to full sun, but not in semi shade or full shade (Elliot and Jones, 1982). Response to salt winds and exposure to full salt spray is reported to be variable (Allen and Allen, 1981; Elliot and Jones, 1982), and plants vary in habitat from sheltered leeward dune slopes to fully exposed headlands.

## Effect of Frost, Drought, and Waterlogging

The altitudinal and large latitudinal range of *A. suaveolens* suggests that this species can tolerate considerable exposure to frost, and Simmons (1966) lists 18-month-old plants as

surviving temperatures as low as -7°C in late June in Tasmania without frost damage.

*A. suaveolens* is particularly common in dry soils, which indicates that this species also has considerable tolerance to drought. However, plants show a much higher death rate during summer than at other times of the year, and Auld (1987) ascribes this to the considerably lower moisture levels of the soil during extended periods of high temperature and low rainfall.

Populations usually occur on freely-draining soils, but can be found on seasonally-waterlogged sites (e.g. Parsons, 1966; Siddiqi *et al.*, 1972; Myerscough and Carolin, 1986) and occasionally in permanently moist areas (e.g. Parsons, 1966; Siddiqi *et al.*, 1976; Benson and Fallding, 1981). However, plants were not recorded as regenerating after fire in ground-water heaths (Siddiqi *et al.*, 1976); and plants have not been recorded from sites where a standing water table reaches the shoot system.

## MORPHOLOGY

The flowers are borne in axillary racemes of heads, these racemes being produced only by buds in the axils of phyllodes on those vegetative shoots that were produced during the previous December to January. Shoots produced in previous years do not usually flower. The axillary primordia may or may not expand and differentiate into floral buds. These floral buds expand lengthwise, the bracts fall off, and the flowers open. These flowers are andromonoecious, with about 13-50% of the flowers being bisexual (Morrison, 1986).

As each individual flower forms, it follows a spiral developmental sequence from the outside to the inside, described in detail by Newman (1936). Each flower is protogynous, the style first being exserted well beyond the petals, which still enclose the contorted undehisced anthers. The style is folded in bud, and pushes its way out between the overlapping petals before the bud opens, straightening progressively as the flower begins to open. The cup-shaped stigma is of the wet non-papillate type, and is sited terminally on the long narrow style. Several days after the exsertion of the style, the stamen filaments unfold and lengthen; although the style still projects well beyond them. The anthers then dehisce. Each flower head in a raceme flowers synchronously, so that each head is also protogynous. However, the racemes open subacropetally and subsynchronously, while the racemes usually open basipetally along the vegetative shoot. Therefore, each raceme and each shoot usually contains flowers at all stages of anthesis at some time.

When the ovary has been fertilized it changes colour from dull brown to reddish-maroon. The unfertilized flowers drop off early, leaving the small fruits on the bare stalks. The fruits then expand very slowly in both length and breadth for 5-8 weeks, after which they rapidly expand in length only for a further 3-5 weeks, before breadth again begins to increase. The fruits reach their final size rapidly after this, and they begin to thicken the fruit walls. The fruits then dry out and open along the ventral and then the dorsal sutures, releasing the seeds. The fruits open about 15-22 weeks after they are formed, with seed release being fairly synchronous in any one population.

The buds that form the next season's vegetative shoots are in the same axils of the phyllodes as the floral buds, and adjacent to them. Thus, the new shoots of one season are the sites of both the ensuing flowering and fruiting and also of the following season's shoot production. If no new vegetative shoots survive on a particular branch of a plant in a particular season, then that branch dies back to a branch that is supporting a surviving shoot. If no new shoots survive on a plant, then that plant dies back to the main stem, where it may or may not produce new shoots from buds that are several years old. Such plants do not usually flower again, and they die the following summer. Therefore, the successful production of new vegetative shoots is the key to the long-term survival of a plant.

If the growing points of the plants are destroyed in any way, reversion foliage consist-

ing of pinnate or bipinnate leaves may appear on the proximal parts of branches or along the stem (Cambage, 1915; 1917; Fletcher, 1920). Similar foliage may be produced at the base of the stem if the upper shoots die back during summer, although this usually consists of small phyllodes with a number of leaflets at the tips. Plants with reversion foliage rarely produce floral buds, and they usually die within the next 3-12 months.

The leaflet buds are often found along the margins of the phyllodes as well as at the tip, resulting in the appearance at different places along the phyllode margins of pairs of reduced pinnae, pairs of leaflets, and single leaflets (Fletcher, 1920).

The phyllodes are xeromorphic microphyllous leaves. The epidermis is narrow, with a thick cuticle (Lemesle, 1965). Most of the mesophyll is composed of chlorenchymatous palisade cells, but it passes gradually into a smaller central zone of spongy cells less rich in chloroplasts (Lsmesle, 1965; Boughton, 1986). The primary and secondary veins are covered by a crescent of sclereid fibres, often with tracheids, and the surrounding tissue sometimes has calcium oxalate inclusions (Lemesle, 1965). The stomata are mesogenous, paracytic and bicytic (Grosso, 1987), fairly large ($25.0 \pm 2.5\mu$m long; Connor and Doley, 1981), and occur on both surfaces of the phyllodes at a density of $249 \pm 21$mm$^{-2}$ (Connor and Doley, 1981).

The woody stems have a perennial vascular cambium, which produces very little secondary phloem. The secondary xylem consists of diffuse porous vessels with paratracheal axial parenchyma. There is no ray parenchyma, and no heartwood is formed. Periderm is present only on older stems very close to the base of the stem.

The contribution to the community biomass (i.e. wood component) in any one area is usually very small (e.g. $< 0.05\%$, Clark, 1975; 0.06-0.09%, Thatcher and Westman, 1975; 0.1%, Specht, 1979), and the percentage cover (i.e. leaf component) is also low (e.g. 0.02- 0.32%, Russell and Parsons, 1978; $> 0.17\%$, Posamentier et al., 1981; 0.7-1.4%, Weste, 1981; 0.2-0.8%, Fox and Fox, 1986). The percentage cover does not apparently show any particular pattern of change with population age (Russell and Parsons, 1978).

## CHROMOSOMES

$2n = 26$ in material from New South Wales (Hamant et al., 1975).

## PHYSIOLOGICAL DATA

Specht and Groves (1966) and Groves and Keriatis (1976) have investigated the phosphorus relations of A. suaveolens in water and sand cultures respectively. The plants showed little growth below 0.1ppm P, but there was a significant increase in dry weight accumulation between 0.1 and 1.0ppm P. No further dry weight increase occurred at 5.0-10.0ppm P, and all plants died at 50ppm P and above. At the higher P levels, root weight showed a greater decrease than did shoot dry weight; and the plants showed toxicity symptoms above P levels of about 4% of the shoot dry weight, with irregular necrotic areas appearing on the phyllodes before they began to die from the tips down. At levels of 50ppm P or more, the cotyledons senesced and the juvenile bipinnate leaves became red-purple, with the pinnae and petioles dying before the formation of phyllodes. At low P levels, $< 30\%$ of the dead leaves were shed and 85-90% of the P was translocated from the dead to the living tissues. The plants did not show any deficiency symptoms at low P levels. The P content of the phyllodes tended to increase with increased P levels in the substrate, and the maximum P uptake from the substrate was 57% (in water culture).

The nitrogen relations of A. suaveolens in sand culture have been investigated by Groves and Keriatis (1976). The plants showed no response to changing N levels from 0-250ppm without the addition of P. The most favourable combination for growth was low P concentration and high N concentration (see also Hannon, 1956). At low N levels the plants

showed deficiency symptoms, with a reddening of the leaflet tips; and the N content of the phyllodes did not vary with the N concentration in the substrate. The root/shoot ratio was highest at intermediate N concentrations with no added P.

Beadle (1962) grew *A. suaveolens* plants in a range of soils in a glasshouse, and found that plants grew larger (ranging from 12 to 170cm tall after 5 months) and produced more leaves on soils with higher nutrient levels (ranging from 23 to 230ppm P). Leaf area did not differ between these treatments. Plants grown on full nutrient solution in the laboratory absorb P far in excess of field requirements (Beadle, 1968); and plants given insoluble phosphate in the form of ground fossil laterite concretions could not absorb this 'unavailable' P (Beadle, 1968).

Clark (1975) and Thatcher and Westman (1975) have shown that the addition of fertilizer to *A. suaveolens* seedlings following sand mining increases their contribution to the community biomass in the following 2-3 years (i.e. bigger plants are produced), but that by the fourth year the species has returned to its pre-mining level. Specht (1975) and Specht *et al.* (1977) have concluded that an increase in the nutrient level in the soil increases the growth rate and speeds-up the life cycle of these plants, resulting in their earlier death; and Specht *et al.* (1977) recorded the disappearance of an unusually high number of *A. suaveolens* plants during the 8 years of their fertilized treatment.

The seeds contain about 0.2% total P, 4.0% total N, 1.0% K, 1.3% Ca, and 0.4% Mg (Beadle, 1968; Groves and Keriatis, 1976; P.J. Myerscough pers. comm.). Phyllodes from field plants contain 0.01-0.05% P (Beadle, 1968; Lambert and Turner, 1987) and 1.8-2.1% N (Hannon, 1956), both increasing with increased nutrient status of the soil, and 0.01% Al, 0.40% Ca, 0.32% Mg, 0.86% K and 1.92% Cl (Lambert and Turner, 1987).

## BIOCHEMICAL DATA

Seneviratne and Fowden (1968) and Evans *et al.* (1977) have found the following free amino acids in the seeds: S-carboxyethylcysteine (the predominant amino acid), S-carboxyethylcysteine sulphoxide, S-carboxyisopropylcysteine, $\beta$-acetyl-$\alpha$,$\beta$-diamino-propionic acid, $\alpha$-amino-$\beta$-ureido-propionic acid, pipecolic acid, 4-hydroxy-pipecolic acid, 5-hydroxypipecolic acid, djenkolic acid, djenkolic acid sulphoxide, $\gamma$-glutamyl-djenkolic acid. Conn *et al.* (1985) did not find any cyanogenic glucosides in either fresh leaves or herbarium material.

## PERENNATION AND REPRODUCTION

*A. suaveolens* is normally a nanophanerophyte, or occasionally a microphanerophyte. Plants without rootstocks have a half-life of 3.7 years (Auld, 1987), with most populations lasting a maximum of 15-25 years (cf. Siddiqi *et al.*, 1976; Specht *et al.*, 1977; Russell and Parsons, 1978; Clemens and Franklin, 1980; Bradstock, 1981; Auld, 1987). The lifespan of the form with rootstocks is unknown. The annual death rate is about 22% up to 8 years of age, and about 12% after this (Auld, 1987).

Vegetative growth continues throughout the life of the plant, with 1-6 shoots being produced each year (Morrison, 1986). Shoot production is low for old plants, and very variable for younger plants (Morrison, 1986), with the younger plants producing much longer shoots (Morrison, 1986).

Reproduction is entirely by seed, although this species can be cultivated from cuttings (Elliot and Jones, 1982). Seedlings are rarely found in the field unless recently stimulated to germinate by a fire (Auld, 1987), with fire-free periods of 10-30 years being the most appropriate for the long-term maintenance of viable populations of this species (Auld, 1987).

## PHENOLOGY

Flowering is strictly seasonal, with floral buds usually initiated in autumn, but with

a distinct geographical sequence from north to south (Table 4). Flowers are most profuse in mid winter, with the fruits ripening and releasing the seeds from late spring to early summer (Table 4).

TABLE 4

*Times at which flowers and mature fruits of* Acacia suaveolens *have been recorded*
*Data from 216 dried specimens at* CBG, MEL, NSW, PERTH, *and* SYD *which had sufficiently detailed data on collection-locality and date, plus Rodway (1903), Ewart (1930), Groves and Specht (1965), Court (1972), Beadle (1976), Armitage (1977), Rogers (1978), Clifford and Specht (1979), Pedley (1979), Whibley (1980), and Beadle et al. (1982)*

| Area | Flowers | Mature fruits |
|------|---------|---------------|
| Queensland | early March — mid August | early June — end October |
| N.S.W. north coast* | mid March — end August | early June — end October |
| N.S.W. central coast and tablelands | mid March — early September | early June — end November |
| N.S.W. south coast + | early April — end October | end June — early December |
| Victoria | end April — end October | early July — mid January |
| South Australia | end May — end September | early September — mid January |
| Tasmania | mid May — mid September | early September — end January |

* north of Newcastle;  + south of Nowra

Flowering time is very population-specific in any one area (Morrison, 1986), but there is considerable variation from year to year, with low rainfall at the beginning of the season delaying the onset of flowering (Morrison, 1986). However, Blakely (1941) suggests that early onset of flowering is also related to low rainfall. Individual plants flower for about 4-7 weeks, but this duration decreases with plant age (Morrison, 1986). Any individual floral bud on a plant flowers for about 3-5 weeks (Morrison, 1986), with most buds opening fairly synchronously.

Fruiting phenology closely follows the flowering phenology (Morrison, 1986), except that fruits ripen and release their seeds over the same 2-3 week period each year, irrespective of when flowering was initiated (Morrison, 1986). Consequently, only early-opening flowers ever ripen fruits, as ripe fruits are usually 15-20 weeks old when they release their seeds (Morrison, 1986).

Vegetative buds are usually initiated immediately after the seeds are released. Vegetative growth continues for 8-10 weeks, when the floral buds are initiated on the new shoots.

Very small numbers of seeds germinate without stimulation from fire, and these may be found at any time of the year (Auld, 1987). Only 14 seedlings emerged at seven sites over three years, and only one of those survived longer than six months (Auld, 1984).

FLOWERING AND POLLINATION

Plants can flower within 1.5 years if germination occurs in summer, but not until the second year if germination occurs in later seasons (cf. Clemens and Franklin, 1980; Benson, 1985); however, individual plants may take up to 4-5 years to flower (Auld, 1984; Benson, 1985). 80-93% of the plants in a population flower each year, and this is consistent from year to year for the life of the population (Morrison, 1986).

Flower production varies greatly from year to year, but there is a close inverse relationship with plant age, the first 1-4 years being the most prolific (Morrison, 1986). This pattern seems to be related to a reduced number of floral buds being produced per vegetative shoot as the plants age (Morrison, 1986), while the large inter-year variation in flower production is related to inter-year variation in the number of vegetative shoots produced (Morrison,

1986). Some plants also appear consistently to produce more flowers each year than do others (Morrison, 1986).

Superimposed on the age pattern is a relationship with rainfall, increased rainfall early in the flowering season being correlated with increased flower production (Morrison, 1986). However, floral buds produced in the middle of the season produce more flowers and ovaries than do floral buds produced early or late in the season (Morrison, 1986), and the ovaries contain more ovules.

Ovule number per ovary is not very variable, being reported as 5-6 (Newman, 1936), 5-7 (Kenrick and Knox, 1982; Knox and Kenrick, 1983), and 6-9 (Morrison, 1986). Anther number per flower is also not very variable, at 60-80 (Newman, 1936), and 44-52 (Morrison,1986). Pollen fertility is fairly high, at 85-95%, but this decreases with plant age (Morrison, 1986).

About 15-31% of the ovaries produced per plant are fertilized, with about 1-12% aborting, and 2-48% being eaten by insects (Morrison, 1986). Of the ovules produced per plant, about 3% are aborted, 12% are eaten, 1% are not fertilized in ovaries that are fertilized, 23% are fertilized, and 61% are dropped from the plant (Morrison, 1986).

Pollination of flowers is very consistent in this species at about 15-31% (Morrison, 1986), and so fruit production closely follows the pattern of flowering discussed above (Morrison, 1986). However, pollination rate is markedly decreased in floral buds opening late in the flowering season (Morrison, 1986).

The pollinators are apparently a range of non-specific insects (Morrison, 1986), including beetles (Coleoptera: Chrysomelidae, Cerambycidae, Apionidae), bees (Hymenoptera: Apidae, Halictidae), flies (Diptera: Syrphidae), ants (Hymenoptera: Formicidae), and hemipterans. However, the introduced honey bee, *Apis mellifera* (Hymenoptera: Apidae), seems to be the most effective pollinator in some areas (Morrison, 1986). Pollen is the only reward, as no nectar is secreted by the phyllode gland (Hardy, 1912; Boughton, 1981; but see also Carne, 1913b). Wind pollination is unlikely, as the 16-grain pollen polyad (see Cookson, 1954; Guinet, 1969; Kenrick and Knox, 1982; Knox and Kenrick, 1983) is not easily windborne.

### SEED PRODUCTION AND DISPERSAL

Of the fruits formed on a plant, about 38-85% abort during the first 5-10 weeks after they are formed, 5-25% abort later on, 2-41% are eaten by insects, and 1-13% mature and release seeds (Morrison, 1986). The abortion of the young fruits apparently allows the plants to regulate tbe number of seeds released per plant quite closely (Morrison, 1986). About 48% of the plants in a population mature fruits in any one year (Auld and Myerscough, 1986), and there is considerable inter-year variability in the number of fruits per plant (Auld and Myerscough, 1986; Morrison, 1986). The number of fruits matured per plant follows the same inverse relationship with plant age as does flower production (Auld and Myerscough, 1986; Morrison, 1986), and there is the same increased production with increased rainfall (Auld and Myerscough, 1986).

Of the seeds formed per plant, about 60% abort while small, 12% abort later, 16% are eaten by insects while small, 7% are eaten by insects later, 3% are consumed by weevil larvae (Coleoptera: Curculionidae), and 2% are matured and released (Morrison, 1986).

The dispersal unit is the seed with its aril. Average seed weights (with aril included) per population of 23-41mg have been reported from a wide geographical range (Specht and Groves, 1966; Beadle, 1968; Groves and Keriatis, 1976; Drake, 1981; Westoby *et al.*, 1982; Auld, 1983; Morrison, 1986), and average weights from 27-41mg have been reported from populations within a few kilometres of each other (Auld, 1983; Morrison, 1986).

The seeds are released passively from the fruits. Auld (1986b) reports that the average distance of fallen seed from the parent plant is 45cm, with 90% of the seed within 1m of the parent. This distance is partly dependent on the height of the parent plant (Auld, 1986b).

Ants have been observed to move seeds to their nests in the Sydney region (Rice and Westoby, 1981; Auld, 1986b), on North Stradbroke Island (Drake, 1981), and on Wilsons Promontory (Andersen and Ashton, 1985). Drake (1981) found seeds to be removed at the rate of 10 seeds in 55 min, with *Rhytidoponera metallica* removing 9 seeds and *Aphaenogaster longiceps* removing the other. Auld (1986b) reports two unidentified species of *Pheidole* and one of *Iridomyrmex* to move seeds, although only *Pheidole* sp.A actually took them into their nests. *Pheidole* sp.A moved seeds an average of about 220cm, while the other two species only moved them about 10-15cm (Auld, 1986b). Removal rates vary from 93-100% (Drake, 1981; Auld, 1986b; Andersen and Ashton, 1985), although Auld (1986b) reported that only 38% of the seed removed by *Pheidole* sp.A was incorporated into the nests, and none of the seed removed by the other two species were. Seeds are found in the top 5cm of the soil outside ant nests, but in the top 2-15cm inside the nests (Auld, 1986b). About 65% of the seeds end up in sites that are unsuitable for germination (Auld, 1987).

All ant species drag the seeds by the tip of the aril. The elaiosome is the folded aril, which in *A. suaveolens* is unusual in being dark brown instead of the more usual whitish colour of other acacias (Vassal, 1971; 1972; Drake, 1981). This elaiosome comprises about 5% of the weight of the dispersal unit (Westoby *et al.*, 1982; Auld, 1984).

The released seeds are incorporated into the soil seed bank, at a density of 6-23 seeds/m$^2$ outside ant nests (Auld, 1986b). The annual decay rate of seeds in the soil is 6.5%, with a seed half-life of 10.7 years (Auld, 1986b). The peak size of the soil seed bank occurs at a population age of about 6 years, and the population self-replacement point (ie. where the number of seeds in the soil equals the initial mature population size) is about 60 years (Auld, 1987).

Dispersal of seeds onto bare rock has also been reported. Five years after an 8-acre [3.2ha] area of Hawkesbury sandstone was cleared of both plant and soil cover to expose the underlying rock, *A. suaveolens* was one of the few species recorded to have become established (Cambage, 1923); and 44 years later plants were reported to be scattered infrequently over the still extremely thin sandy soil (Hannon and Evans, 1963).

## Viability of Seeds and Germination

Staining with 2,3,5-triphenyl-tetrazolium chloride reveals that mature seeds heavier than 20mg are more than 98% viable, independent of site or age of the parent plant (Auld, 1986a). Seeds less than this weight have significantly reduced viability (down to 40%). The seeds have a hard impermeable seed coat 180µm thick (Cavanagh, 1980), which means that the seeds are in induced dormancy (*sensu* Harper, 1977). Less than 1% of the mature seeds will germinate spontaneously on release from the fruit, and the remainder enter the soil seed bank (Auld, 1986a). Most of the induced dormancy is acquired during the first 2 weeks after seed release (Auld, 1986a).

The seeds can remain viable in storage for many years. P. J. Myerscough (pers. comm.) found that after 83 months storage 16/23 seeds were still capable of imbibing after scarification and treatment with boiling water, and Ewart (1908) reported that 1/25 seeds stored for 51 years was still capable of imbibing after sulphuric acid treatment.

The seed coat impermeability can be overcome by heating (either by adding boiling water, heating in an oven, or exposure to microwaves), treatment with sulphuric acid and dilute ammonia or lime water, or mechanical chipping or abrading (Ewart, 1908; Clemens *et al.*, 1977; Cavanagh, 1980; Auld, 1986c). Clemens *et al.* (1977) achieved maximum germination of 77% by chipping the seeds, while Auld (1986a) achieved 98% germination

by abrading with sandpaper. For mechanical chipping, seeds germinate more rapidly, with a maximum rate of 48.5 seeds/day as opposed to only 2.2 seeds/day for the boiling water treatment (Clemens et al., 1977). Seeds imbibe within 15 hours when mechanically chipped (Clemens et al., 1977). The optimum temperatures for breaking seed dormancy are 60-80°C, for any length of time (Clemens et al., 1977; Auld, 1986c). Below this temperature, germination percentage is low, even if heated for long periods of time, and above this the seeds are killed even if exposed for short periods.

Cavanagh (1980) considers the strophiole to be responsible for overcoming the hard-seededness. He found that, after heating the seeds to 100°C by microwave exposure, the shortened palisade cells covering the vascular bundle at the strophiole broke down, allowing water penetration in this area. The seeds then swelled from this end. Heat-treated seeds that had the strophiole covered with petroleum jelly did not imbibe, and so there is no general water permeability after treatment.

Heat-treated seeds have been observed to germinate and emerge from depths of up to 10-15cm in laboratory trials (Drake, 1981; Auld, 1986c); but in the field, emergence has only been recorded from a maximum depth of 6cm (mean depth 2.4cm) (Auld, 1986c).

## SEEDLING MORPHOLOGY

Seedling growth in *A. suaveolens* has been monitored and described in detail by Cambage (1915) (see his fig. 1, fig. 3, plate IX nos 8-10) and more recently by Vassal (1970; 1972).

After germination, the curved upper portion of the hypocotyl appears above the soil first, the cotyledons free themselves from the testa, and then the hypocotyl elongates and becomes erect, pulling the cotyledons out of the soil, where they open out. The hypocotyl is erect, terete, pale reddish-violet, 5-40mm long, thicker than the epicotyl, with their boundary marked by an annular crest. The cotyledons are opposite, shortly (but distinctly) petiolate, oblong, distinctly lobed, sagittate, 6-9mm long, 3-4mm wide, erect at first but becoming horizontal in a few days, reddish-violet on the lower surface, greenish-brown becoming greenish-red then green on the upper surface. They are persistent at least until the production of the 15-16th leaves.

The first leaf produced is pinnate, followed by a succession of alternate, bipinnate leaves, phyllodinization beginning at the 5-8th leaf stage and ending between the 7-12th leaves. The first two leaves are produced at right angles to the plane of the cotyledons, and subsequent leaves appear in two helices. This pattern does not change with the transition to phyllodes. The first leaf is usually 5-7mm long, and is a similar colour to the cotyledons. Subsequent leaves sequentially increase from 1-2cm to 3-4cm long, and are pale green. The early leaves are lyrate, with the number of leaflets sequentially increasing from (2-)3-4 (-5) to 4-6(-7), before phyllodinization. Up to the 4th leaf stage, mixed leaves are sometimes produced, where the proximal pair of leaflets may be replaced by a pair of pinnae which are as large as the distal part of the leaf. The phyllodes appear gradually as the petioles in subsequent leaves become more dilated vertically, with reducing numbers of leaflets at the tips.

## MYCORRHIZA

Rhizobial root nodules have been reported on this species in the field in the Sydney region (Carne, 1913a; Benjamin, 1915; Hannon, 1956; Norris, 1959; Barnet et al., 1985) and in Queensland (Bowen, 1956). Thess rhizobia are of the slow-growing *Bradyrhizobium* type (Norris, 1959; Barnet et al., 1985) as well as the fast-growing *Rhyzobium* type (Barnet et al., 1985). The nodules can produce a urea-splitting enzyme (Benjamin, 1915). In cultivation, the bacteria show increased growth with increased Mg in the medium (Norris, 1959); and

root nodulation decreases with increasing N levels in the substrate (Groves and Keriatis, 1976), but increases with added P at low N levels (Hannon, 1956; Beadle, 1962).

## ANIMAL FEEDERS AND PARASITES

The fruits of *A. suaveolens* are reported to be an important food source for lorikeets, parrots, cockatoos, and native pigeons (Adams, 1980), although evidence has been presented only for crimson rosellas [*Platycercus elegans* (Gmelin) ], which cut the edge from the unripe pod to extract the half-ripe seed.

The only invertebrates reported to be associated with *A. suaveolens* are insects. Froggatt (1902) reports that larvae of *Rhinotia hoemoptera* Kirby (Coleoptera: Bruchidae) live inside the branches, while the adults feed in the foliage. Also, *Sextius virescens* (Faimaire) (Homoptera: Membracidae) lay their eggs in slits cut through the bark of young branches (Cookson and New, 1980). New (1983) reports 11 unidentified species of arthropods inhabiting 18-month-old seedlings, 3 of these species being Araneae, 2 Coleoptera, and 1 Lepidoptera.

Morrison (1986) reports unidentified beetles (Coleoptera: Chrysomelidae) and grasshoppers (Orthoptera: Acrididae) consuming flowers.

Auld (1983), Auld (1986d) and Auld and Myerscough (1986) report that larvae of *Melanterius corosus* (Boisduval) (Coleoptera: Curculionidae) feed in developing seeds in the field, as well as consuming whole fruits. Auld (1986d) also reports that adults of *Melanterius maculatus* Lea will oviposit in fruits in the laboratory. Auld (1983) and Auld and Myerscough (1986) report unidentified lepidopterans, hemipterans, and grasshoppers feeding on all or part of developing fruits, while Morrison (1986) lists unidentified species of adult grasshoppers (Orthoptera: Acrididae), sap-suckers (Hemiptera: Psyllidae), and beetles (Coleoptera: Chrysomelidae) doing the same. Morrison (1986) also notes several unidentified species of coleopteran larvae (Coleoptera: Lagriidae, Pythidae, Tenebrionidae, Nitidulae), and five unidentified species of lepidopteran larvae, all eating developing fruits.

Drake (1981) reports *Aphaenogaster longiceps* F. Smith and *Rhytidoponera metallica* F. Smith (Hymenoptera: Formicidae) eating the aril of mature seeds, while Auld (1986b) reports two species of *Pheidole* and one of *Iridomyrmex* to do the same.

## PLANT DISEASES AND PARASITES

Weste and Law (1973) and Weste (1981) consider *A. suaveolens* to be a species which is tolerant of *Phytophthora cinnamomi* Rands rather than resistant to it. In their study plots on Wilsons Promontory, the species did not show early signs of becoming affected by the root rot, unlike the majority of the surrounding woodland (Weste and Law, 1973), but did eventually develop mild but fluctuating symptoms (Weste, 1981). While the surrounding community changed from a low shrub woodland to an open sedge woodland, with a reduction in tree density and a loss of susceptible species, *A. suaveolens* was the only species to actually increase in percentage frequency. On the diseased plots, *A. suaveolens* plants showed severe and permanent die-back during periods of high evaporation and low rainfall, while on the control plots no die-back occurred. This behaviour may merely be a response to the opening of the tree canopy.

Fletcher (1920) records that *A. suaveolens* plants are 'particularly liable to fungoid attacks, which sometimes interfere with, or even kill the growing point', but he does not specify the fungi involved. Similarly, Cambage (1917) comments on 'pathological trouble' at the growing points but is not specific.

## HISTORY AND CONSERVATION

*A. suaveolens* was first collected by Joseph Banks and Daniel Solander at Botany Bay in 1770 (Britten, 1905), and it was among the first species to have seeds sent back to Europe

from Australia (Lebler, 1980), so that by the end of that century it had been established in a number of the botanical gardens of Britain (Loudon, 1830) and Europe (e.g. Jacquin, 1798). The only report of the direct human exploitation of *A. suaveolens* is the use by the early European settlers of the aromatic leaves in infusions as teas (Nakao, 1976). The pre-history is unknown, as no pollen directly referrable to *A. suaveolens* has been found in the fossil record.

A. suaveolens was apparently common throughout its geographical range when it was first collected by Europeans, as it was readily collected by many of the early exploration parties. However, it is now much more restricted in occurrence in Queensland, Victoria, South Australia, and Tasmania due to human destruction of suitable habitats (Morrison *et al.*, 1983).

In Queensland, populations are now rare, principally because of the many new coastal housing developments that are occupying the available habitats (Morrison *et al.*, 1983). The only areas where this species appears not to be at risk are the less-disturbed parts of the large sand islands.

In Victoria, there are apparently no longer any large coastal populations west of Wilsons Promontory, although this species was frequently collected between there and Melbourne at the turn of the century (Morrison *et al.*, 1983). This appears to be a result of pastures and settlements encroaching on the somewhat restricted habitats.

In South Australia, this species has only been recorded since the early 1960's, and the majority of the known populations are in vacant lots in plantations (Morrison *et al.*, 1983). More recently, the western-most known population was apparently destroyed by roadside vegetation clearing.

In Tasmania, this species is also rarely encountered, principally due to destruction of coastal heathlands. In particular, the species' distribution along the northern and eastern coastlines is now very patchy.

The species is most widespread and common in New South Wales, and it is very easily located along most of the coastal areas. In particular, even in the disturbed urban areas *A. suaveolens* is commonly encountered in the coastal parts, unlike the other states.

The two geographically-restricted morphological forms are each present in conservation areas, the narrow-leaved form in the Myall Lakes National Park, and the Grampians form in the Grampians National Park.

*References*

ADAM, G. M., 1980. — *Birdscaping Your Garden.* Sydney: Rigby.
ALLEN, O. N., and ALLEN, E. K., 1981. — *The Leguminosae, A Source Book of Characteristics, Uses, and Nodulation.* Wisconsin: University of Wisconsin Press.
ANDERSEN, A. N., and ASHTON, D. H., 1985. — Rates of seed removal by ants at heath and woodland sites in southeastern Australia. *Aust. J. Ecol.* 10: 381-390.
ANON., 1941. — The Biological Flora of the British Isles. *J. Ecol.* 29: 356-361.
ARMITAGE, I., 1977. — *Acacias of New South Wales.* Sydney: NSW Region of the Society for Growing Australian Plants.

ASHTON, D. H., and WEBB, R. N., 1977. — The ecology of granite outcrops at Wilson's Promontory, Victoria. *Aust. J. Ecol.* 2: 269- 296.

AULD, T. D., 1983. — Seed predation in native legumes of south-eastern Australia. *Aust. J. Ecol.* 8: 367-376.

——, 1984. — Population Dynamics of *Acacia suaveolens* (Sm.) Willd. Sydney: University of Sydney, Ph.D. thesis, unpubl.

——, 1986a. — Dormancy and viability in *Acacia suaveolens* (Sm.) Willd. *Aust. J. Bot.* 34: 463-472.

——, 1986b. — Population dynamics of the shrub *Acacia suaveolens* (Sm.) Willd.: Dispersal and the dynamics of the soil seed bank. *Aust. J. Ecol.* 11: 235-254.

——, 1986c. — Population dynamics of the shrub *Acacia suaveolens* (Sm.) Willd.: Fire and the transition to seedlings. *Aust. J. Ecol.* 11: 373-385.

——, 1986d. — Variation in predispersal seed predation in several Australian *Acacia* spp. *Oikos* 47: 319-326.

——, 1987. — Population dynamics of the shrub *Acacia suaveolens* (Sm.) Willd.: Survivorship throughout the life cycle, a synthesis. *Aust. J. Ecol.* 12: 139-151.

——, and MYERSCOUGH, P. J., 1986. — Population dynamics of the shrub *Acacia suaveolens* (Sm.) Willd.: Seed production and predispersal seed predation. *Aust. J. Ecol.* 11: 219-234.

AUSTRALIAN BUREAU OF METEOROLOGY, 1975a-e. — *Climatic Averages. Queensland. New South Wales. Victoria. South Australia and Northern Territory. Tasmania and Miscellaneous.* Canberra: Government Printer.

BARNET, Y. M., CATT, P. C., and HEARNE, D. H., 1985. — Biological nitrogen fixation and root-nodule bacteria (*Rhizobium* sp. and *Bradyrhizobium* sp.) in two rehabilitating sand dune areas planted with *Acacia* spp. *Aust. J. Bot.* 33: 595-610.

BEADLE, N. C. W., 1962. — Soil phosphate and the delimitation of plant communities in eastern Australia II. *Ecology* 43: 281-288.

——, 1968. — Some aspects of the ecology and physiology of Australian xeromorphic plants. *Aust. J. Sci.* 30: 348-355.

——, 1976. — *Students Flora of North Eastern New South Wales.* Part III. Armidale: University of New England Printery.

——, 1981. — *The Vegetation of Australia.* Cambridge: Cambridge University Press.

——, EVANS, O. D., and CAROLIN, R. C., 1982. — *Flora of the Sydney Region.* 3rd ed. Sydney: A. H. and A. W. Reed.

BEAUGLEHOLE, A. C., 1980a. — Erroneous or doubtful Victorian vascular plant grid records. *Victorian Nat.* 97: 213-216.

——, 1980b. — *Victorian Vascular Plant Checklists.* Portland: Western Victorian Field Naturalists Clubs Association.

BENJAMIN, M. S., 1915. — A note on the occurrence of urease in legume nodules and other plant parts. *J. Proc. R. Soc. N.S.W.* 49: 78-80.

BENSON, D. H., 1981a. — Vegetation of upper Mangrove Creek, Wyong, New South Wales. *Cunninghamia* 1: 7-22.

——, 1981b. — Vegetation of Lion Island, Broken Bay, New South Wales. *Cunninghamia* 1: 121-123.

——, 1985. — Maturation periods of fire-sensitive shrub species in Hawkesbury Sandstone vegetation. *Cunninghamia* 1: 339-349.

BENSON, J. S., and FALLDING, H., 1981. — Vegetation survey of Brisbane Water National Park and environs. *Cunninghamia* 1: 79-113.

BLAKELY, W. F., 1941. — Notes on some winter-flowering wattles. *Aust. Nat.* 11(1): cov. iii.

BOUGHTON, V. H., 1981. — Extrafloral nectaries of some Australian phyllodineous acacias. *Aust. J. Bot.* 29: 653-664.

——, 1986. — Phyllode structure, taxonomy and distribution in some Australian acacias. *Aust. J. Bot.* 34: 663-674.

BOWEN, G. D., 1956. — Nodulation of legumes indigenous to Queensland. *Qd J. agric. Sci.* 13: 47-60.

BRADSTOCK, R., 1981. — Our phoenix flora. *Aust. nat. Hist.* 20: 223-226.

BRITTEN, J., (ed.), 1905. — *Illustrations of the Botany of Captain Cook's Voyage Round the World in H.M.S. Endeavour in 1768-71.* Part I. London: Trustees of the British Museum.

BUCHANAN, R. A., and HUMPHREYS, G. S., 1980. — The vegetation of two podzols on the Hornsby Plateau, Sydney. *Proc. Linn. Soc. N.S.W.* 104: 49-71.

BURROUGH, P. A., BROWN, L., and MORRIS, E. C., 1977. — Variations in vegetation and soil pattern across the Hawkesbury Sandstone plateau from Barren Grounds to Fitzroy Falls, New South Wales. *Aust. J. Ecol.* 2: 137-159.

CAMBAGE, R. H., 1915. — *Acacia* seedlings, Part I. *J. Proc. R. Soc. N.S.W.* 49: 81-121.

——, 1917. — *Acacia* seedlings, Part II. *J. Proc. R. Soc. N.S.W.* 51: 389-409.

——, 1923. — Plant invasion of a denuded area. *J. Proc. R. Soc. N.S.W.* 57: 334-336.

CARNE, W. M., 1913a. — Notes on some forms of association amongst plants, particularly in regard to bacterial nodules and mycorrhizae in Australian plants. *Aust. Nat.* 2: 192-198.

——, 1913b. — The secretion of nectar by extra-floral glands in the genus *Acacia* (wattles). *Aust. Nat.* 2: 198-199.

CAVANAGH, A. K., 1980. — A review of some aspects of the germination of acacias. *Proc. R. Soc. Vict.* 91: 161-180.

CHURCHILL, D. M., and DE CORONA, A., 1972. — *The Distribution of Victorian Plants.* North Blackburn: Dominion Press.

CLARK, S. S., 1975. — The effect of sand mining on coastal heath vegetation in New South Wales. *Proc. Ecol. Soc. Aust.* 9: 1-16.

CLEMENS, J., and FRANKLIN, M. H., 1980. — A description of coastal heath at North Head, Sydney Harbour National Park: impact of recreation and other disturbance since 1951. *Aust. J. Bot.* 28: 463-478.

——, JONES, P. G., and GILBERT, N. H., 1977. — Effect of seed treatments on germination in *Acacia. Aust. J. Bot.* 25: 269-276.

CLIFFORD, H. T., and SPECHT, R. L., 1979. — *The Vegetation of North Stradbroke Island, Queensland.* St Lucia: University of Queensland Press.

CONN, E. E., MASLIN, B. R., CURRY, S., and CONN, M. E., 1985. — Cyanogenesis in Australian species of *Acacia.* Survey of herbarium specimens and living plants. *West. Aust. Herb. Res. Notes* 10: 1-60.

CONNOR, D. J., and DOLEY, D., 1981. — The water relations of heathlands: physiological adaptations to drought. *In:* SPECHT, R. L., (ed.), *Ecosystems of the World.* Vol. 9B. *Heathlands and Related Shrublands, Analytical Studies:* 131-141. Amsterdam: Elsevier.

COOKSON, I. C., 1954. — The Cainozoic occurrence of *Acacia* in Australia. *Aust. J. Bot.* 2: 52-59.

COOKSON, L., and NEW, T. R., 1980. — Observations on the biology of *Sextius virescens* (Faimaire) (Homoptera, Membracidae) on *Acacia* in Victoria. *Aust. entomol. Mag.* 7: 4-10.

COSTERMANS, L. F., 1981. — *Native Trees and Shrubs of South-Eastern Australia.* Melbourne: Rigby.

COURT, A. B., 1972. — Mimosaceae. *In:* WILLIS, J. H., *A Handbook to Plants in Victoria.* Vol. II: 211-245. Melbourne: Melbourne University Press.

DAVIS, C., 1941a. — Plant ecology of the Bulli District. Part II: Plant communities of the plateau and scarp. *Proc. Linn. Soc. N.S.W.* 66: 1-19.

——, 1941b. — Plant ecology of the Bulli District. Part III: Plant communities of the coastal slopes and plain. *Proc. Linn. Soc. N.S.W.* 66: 20-32.

DRAKE, W. E., 1981. — Ant-seed interactions in dry sclerophyll forest on North Stradbroke Island, Queensland. *Aust. J. Bot.* 29: 293-309.

DURRINGTON, L. R., 1977. — *Vegetation of Moreton Island.* Qd Dept. Prim. Ind. Botany Branch Tech. Bull. No. 1.

ELLIOT, W. R., and JONES, D. L., 1982. — *Encyclopaedia of Australian Plants Suitable for Cultivation.* Vol. 2. Melbourne: Lothian.

EVANS, C. S., QUERESHI, M. Y., and BELL, E. A., 1977. — Free amino acids in the seeds of *Acacia* species. *Phytochemistry* 16: 565-570.

EWART, A. J., 1908. — On the longevity of seeds. *Proc. R. Soc. Vict.* 21: 1-210.

——, 1930. — *Flora of Victoria.* Melbourne: Government Printer.

FALLDING, H., and BENSON, J. S., 1985. — Natural vegetation and settlement at Macquarie Pass, Illawarra region, New South Wales. *Cunninghamia* 1: 285-311.

FIRTH, M. J., 1969. — Flora of Rocky Cape. *Rec. Queen Vict. Mus.* 33: 1-16.

FLETCHER, J. J., 1920. — On the correct interpretation of the so-called phyllodes of the Australian phyllodineous acacias. *Proc. Linn. Soc. N.S.W.* 45: 24-47.

FORBES, S. J., WALSH, N. G., and GULLAN, P. K., 1982. — Vegetation of east Gippsland. *Muelleria* 5: 53-113.

FOX, M. D., and FOX, B. J., 1986. — The effect of fire frequency on the structure and floristic composition of a woodland understorey. *Aust. J. Ecol.* 11: 77-85.

FROGGATT, W. W., 1902. — Insects of the wattle trees. *Agric. Gaz. N.S.W.* 13: 701-720.

GILLHAM, M. E., 1960. — Destruction of indigenous heath vegetation in Victoria by sea-bird colonies. *Aust. J. Bot.* 8: 277-317.

GROSSO, B., 1987. — A first contribution to the study of stomatal types in the genus *Acacia. Bull. int. Group study Mimosoideae* 14: 53-64.

GROVES, R. H., and KERIATIS, K., 1976. — Survival and growth of seedlings of three sclerophyllous species at high levels of phosphorus and nitrogen. *Aust. J. Bot.* 24: 681-690.

——, and SPRECHT, R. L., 1965. — Growth of heath vegetation I. Annual growth curves of two heath ecosystems in Australia. *Aust. J. Bot.* 13: 261-280.

GUINET, Ph., 1969. — Les Mimosacées. Étude de palynologie fondamentale, corrélations, évolution. *Trav. Sect. scient. tech. Inst. fr. Pondichéry* 9: 1-293.

HAMANT, C., LESCANNE, N., and VASSAL, J., 1975. — Sur quelques nombres chromosomiques nouveaux dans le genre *Acacia. Taxon* 24: 667-670.

HANNON, N. J., 1956. — The status of nitrogen in the Hawkesbury Sandstone soils and their plant communities in the Sydney district. I. The significance and level of nitrogen. *Proc. Linn. Soc. N.S.W.* 81: 119-143.

——, and EVANS, O. D., 1963. — The regeneration of plant cover on a denuded sandstone area. *Proc. Linn. Soc. N.S.W.* 88: 47-53.

HARDY, A. D., 1912. — The distribution of leaf glands in some Victorian acacias. *Victorian Nat.* 29: 26-32.

HARPER, J. L., 1977. — *Population Biology of Plants.* London: Academic Press.

HARRIS, S., and KIRKPATRICK, J. B., 1982. — The vegetation of Schouten Island, Tasmania. *Pap. Proc. R. Soc. Tasm.* 116: 117-141.

HARROLD, A., 1979. — Heathland regeneration after fire at Noosa. *Qld Nat.* 22: 88-96.

HOLMGREN, P. K., KEUKEN, W., and SCHOFIELD, E. K., 1981. — *Index Herbariorum.* Part I. *The Herbaria of the World.* The Hague: W. Junk.

INGWERSEN, F., 1976. — *Vegetation of the Jervis Bay Territory.* Dept. Cap. Terr. Conserv. Ser. No. 3.

JACOBS, S. W. L., and PICKARD, J., 1981. — *Plants of New South Wales.* Sydney: National Herbarium of N.S.W.

JACQUIN, N. J. VON, 1798. — *Plantarum Rariorum Horti Caesarei Schoenbrunnensis.* Vol. 3. Vienna: C. F. Wappler.

KENRICK, J., and KNOX, R. B., 1982. — Function of the polyad in reproduction in *Acacia. Ann. Bot.* 50: 721-727.

KIRKPATRICK, J. B., 1973. — The vegetation of Sloping Island, Tasmania. *Victorian Nat.* 90: 312-321.

——, 1975. — Phytosociological analysis of the vegetation of Lagoon Beach, Tasmania. *Pap. Proc. R. Soc. Tasm.* 109: 53-63.

——, 1977a. - Native vegetation of the west coast region of Tasmania. *In:* BANKS, M. R., and KIRKPATRICK, J. B., (eds), *Landscape and Man*: 55-80. Hobart: Royal Society of Tasmania.

——, 1977b. — *The Disappearing Heath.* Hobart: Tasmanian Conservation Trust.

KNOX, R. B., and KENRICK, J., 1983. — Polyad function in relation to the breeding system of *Acacia. In:* MULCAHY, D. L., and OTTAVIANO, E. (eds), *Pollen: Biology and Implications for Plant Breeding*: 411-417. New York: Elsevier.

LAMBERT, M. J., and TURNER, J., 1987. — Suburban development and change in vegetation nutritional status. *Aust. J. Ecol.* 12: 193-196.

LEBLER, B., 1980. — The wattles of south-eastern Queensland. Phyllodes with one prominent vein and heads in axillary racemes. *Qld Agric. J.* 106: 127-144.

LEMESLE, R., 1965. — Contribution à l'étude histologique des phyllodes chez les *Acacia* Australiens. *Revue gen. Bot.* 70: 235-256.

LOUDON, J. C., (ed.), 1830. — *An Encyclopaedia of Plants.* London: Longman.

MASLIN, B. R., and PEDLEY, L., 1982. — The distribution of *Acacia* (Leguminosae: Mimosoideae) in Australia. Part 1. Species distribution maps. *West. Aust. Herb. Res. Notes* 6: 1-128.

MCDONALD, W. J. F., and ELSOL, J. A., 1984. — *Moreton Region Vegetation Map Series Summary Report and Checklist for Caloundra, Brisbane, Beenleigh and Murwillumbah.* Brisbane: Qd Dept. Prim. Ind.

MILLER, P. R., 1972. — Vegetation Associations in Royal National Park. Sydney: University of Sydney, B.Sc.(Hons) thesis, unpubl.

MORRISON, D. A., 1986. — A Demographic Analysis of Reproduction in *Acacia suaveolens* (Smith) Willd. (Mimosaceae), Sydney: University of Sydney, Ph.D. thesis, unpubl.

MORRISON, D., AULD, T., and GALLAGHER, K., 1983. — The distribution, ecology and conservation status of *Acacia suaveolens. Victorian Nat.* 100: 140-145.

MYERSCOUGH, P. J., and CAROLIN, R. C., 1986. — The vegetation of the Eurunderee sand mass, headlands, and previous islands in the Myall Lakes area, New South Wales. *Cunninghamia* 1: 399-466.

NAKAO, S., (ed.), 1976. — *Tanaka's Cyclopedia of Edible Plants of the World.* Tokyo: Keigaku Publishing Co.

NEW, T. R., 1983. — Colonisation of seedling acacias by arthropods in southern Victoria. *Aust. entomol. Mag.* 10: 13-18.

NEWMAN, I. V., 1936. — Studies in the Australian acacias. VI. The meristematic activity of the floral apex of *Acacia longifolia* and *Acacia suaveolens* as a histogenetic study of the ontogeny of the carpel. *Proc. Linn. Soc. N.S.W.* 61: 56-88.

NORRIS, D. O., 1959. — The role of calcium and magnesium in the nutrition of *Rhizobium. Aust. J. agric. Res.* 10: 651-698.

OPIE, A. M., GULLAN, P. K., VAN BERKEL, S. C., and VAN REES, H., 1984. — Vegetation of the Western Port catchment. *Muelleria* 5: 289-346.

OUTHRED, R., LAINSON, R., LAMB, R., and OUTHRED, D., 1985. — A floristic survey of Ku-Ring-Gai Chase National Park. *Cunninghamia* 1: 313-338.

PARSONS, R. F., 1966. — The soils and vegetation of Tidal River, Wilson's Promontory. *Proc. R. Soc. Vict.* 79: 319-354.

PEDLEY, L., 1979. — A revision of *Acacia* Mill. in Queensland (concluded). *Austrobaileya* 1: 235-337.

PETRIE, A. H. K., 1925. — An ecological study of the flora of Mount Wilson. Part ii. The *Eucalyptus* forests. *Proc. Linn. Soc. N.S.W.* 50: 145-166.

PIDGEON, I. M., 1938. — The ecology of the central coastal area of New South Wales. II. Plant succession on the Hawkesbury Sandstone. *Proc. Linn. Soc. N.S.W.* 63: 1-26.

——, 1940. — The ecology of the central coastal area of New South Wales. III. Types of primary succession. *Proc. Linn. Soc. N.S.W.* 65: 221-249.

POSAMENTIER, H. G., CLARK, S. S., HAIN, D. L., and RECHER, H. F., 1981. — Succession following wildfire in coastal heathland (Nadgee Nature Reserve, N.S.W.). *Aust. J. Ecol.* 6: 165-175.

RICE, B., and WESTOBY, M., 1981. — Myrmecochory in sclerophyll vegetation of the West Head, New South Wales. *Aust. J. Ecol.* 6: 291-298.

RODWAY, L., 1903. — *The Tasmanian Flora.* Hobart: Government Printer.

ROGERS, F. J. C., 1978. — *A Field Guide to Victorian Wattles.* 2nd ed. Australia: Brown, Prior and Anderson.

RUSSELL, R. P., and PARSONS, R. F., 1978. — Effects of time since fire on heath floristics at Wilson's Promontory, southern Australia. *Aust. J. Bot.* 26: 53-61.

SENEVIRATNE, A. S., and FOWDEN, L., 1968. — The amino acids of the genus *Acacia. Phytochemistry* 7: 1039-1045.

SHARPE, P. R., and BATIANOFF, G. N., 1985. — Mt Coolum checklist of ferns, conifers and flowering plants. *Qd Nat.* 25: 57-74.

SIDDIQI, M. Y., CAROLIN, R. C., and ANDERSON, D. J., 1972. — Studies in the ecology of coastal heath in New South Wales. I. Vegetation structure. *Proc. Linn. Soc. N.S.W.* 97: 211-224.

——, ——, and MYERSCOUGH, P. J., 1976. — Studies in the ecology of coastal heath in New South Wales. III. Regrowth of vegetation after fire. *Proc. Linn. Soc. N.S.W.* 101: 53-63.

SIMMONS, M., 1966. — Frost hardy natives. - 2. *Aust. Pl.* 3: 275, 287.

——, 1981. — *Acacias of Australia.* Melbourne: Nelson.

SPECHT, R. L., 1970. — Vegetation. *In:* LEEPER, G. W., (ed.), *The Australian Environment.* 4th ed: 44-67. Melbourne: Melbourne University Press.

——, 1972. — *The Vegetation of South Australia.* 2nd ed. Adelaide: Government Printer.

——, 1975. — The effect of fertilizers on sclerophyll (heath) vegetation — the problems of revegetation after sandmining of high dunes. *Search* 6: 459-461.

——, 1979. — The sclerophyllous (heath) vegetation of Australia: The eastern and central states. *In:* SPECHT, R. L., (ed.), *Ecosystems of the World.* Vol. 9A. *Heathlands and Related Shrublands. Descriptive Studies:* 125-210. Amsterdam: Elsevier.

——, CONNOR, D. J., and CLIFFORD, H. T., 1977. — The heath-savannah problem: the effect of fertilizer on sand-heath vegetation of North Stradbroke Island, Queensland. *Aust. J. Ecol.* 2: 179-186.

——, and GROVES, R. H., 1966. — A comparison of the phosphorus nutrition of Australian heath plants and introduced economic plants. *Aust. J. Bot.* 14: 201-221.

THATCHER, A. C., and WESTMAN, W. E., 1975. — Succession following mining on high dunes of coastal southeast Queensland. *Proc. Ecol. Soc. Aust.* 9: 17-33.

VASSAL, J., 1970. — Contribution à l'étude de la morphologie des plantules d'*Acacia.* Acacias insulaires des Oceans Indien et Pacifique: Australie, Formose, Iles Maurice et Hawaii. *Bull. Soc. hist. nat. Toulouse* 106: 191-276.

——, 1971. — Contribution à l'étude morphologique des grains d'*Acacia. Bull. Soc. hist. nat. Toulouse* 107: 191-246.

——, 1972. — Apport des recherches ontogéniques et séminologiques à l'étude morphologique, taxonomique et phylogénique du genre *Acacia. Bull. Soc. Hist. nat. Toulouse* 108: 125-247.

WEBB, J. B., 1981. — Vegetation of Spectacle Island, Hawkesbury River, New South Wales. *Cunninghamia* 1: 115-119.

WEST, G., 1981. — Changes in the vegetation of sclerophyll shrubby woodland associated with invasion by *Phytophthora cinnamomi. Aust. J. Bot.* 29: 261-276.

——, and LAW, C., 1973. — The invasion of native forest by *Phytophthora cinnamomi.* III. Threat to the National Park, Wilson's Promontory, Victoria. *Aust. J. Bot.* 21: 31-51.

WESTOBY, M., RICE, B., SHELLEY, J. M., HAIG, D., and KOHEN, J. L., 1982. — Plants' use of ants for dispersal at West Head, New South Wales. *In:* BUCKLEY, R. C., (ed.), *Ant-Plant Interactions in Australiaa:* 75-87. The Hague: W. Junk.

WHIBLEY, D. J .E., 1980. — *Acacias of South Australia.* Adelaide: Government Printer.

WHITE, C. T., 1945. — Wattles or acacias of the Brisbane district. *Qd Nat.* 12: 107-113.

YATES, D. B., 1976. — Some Effects of Disturbance of Vegetation Beneath Electrical Transmission Lines. Sydney: University of Sydney, B.Sc.(Hons) thesis, unpubl.